CLASSIFICATION OF THE MIDDLE AMERICAN GENUS *CYRTOLAUS* BATES (COLEOPTERA: CARABIDAE: PTEROSTICHINI)

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Based on synapotypic characteristics of mouthparts and male genitalia, overall similarity in structure and form, and geographical proximity, the Middle American Cyrtolaus *Bates (type species* C. furculifer *Bates) and* Ithytolus *Bates (type species* I. anomalus *Bates* = Pterostichus orizabae *Csiki) are treated as subgenera of a single genus, and are included in a new monobasic subtribe of Pterostichini: Cyrtolaina. Five new species are described and lectotypes are selected as required for the previously described ones. Range maps and illustrations of habitus and male genitalia are provided. Included in* Ithytolus *is* C. orizabae *Csiki. The subgenus* Cyrtolaus *includes eight species:* C. lobipennis *Bates;* C. subiridescens *new species (type locality 6.6 mi. n. Pueblo Nuevo, Chiapas);* C. brevispina *new species (type locality Yerba Buena Mission, 1.5 mi. n. Pueblo Nuevo, Chiapas);* C. newtoni *new species (type locality 22.4 mi. s. Valle Nacional, Oaxaca);* C. ricardo *new species (type locality Volcan Tacaná, near Union Juarez, Chiapas);* C. spinicauda *Bates;* C. furculifer *Bates; and* C. grumufer *new species (type locality Yerba Buena Mission, 1.5 mi. n. Pueblo Nuevo, Chiapas). The species inhabit montane forests. A reconstructed phylogeny is provided, with the sequence of relationships indicated by the sequence of species names, as listed above. It is proposed that the pattern of geographical distribution and morphological differentiation is the result of alternating periods of isolation in, and dispersals among the mountain systems of Guatemala and southern Mexico.*

En nous basant sur les caractéristiques synapotypiques des pieces bucales et les organes génitaux mâles, sur les similarités généralles de la structure et de la forme, et la proximité géographique, nous traitons comme sous-genre d'un seul genre les Cyrtolaus *Bates (espèce typique* C. furculifer *Bates) et les* Ithytolus *Bates (espèce typique* I. anomalus *Bates* = Pterostichus orizabae *Csiki), et nous les incluons dans une nouvelle sous-tribu monobasique des Pterostichini: Cyrtolaina. Nous avons décrit cinq nouvelles espèces et nous avons sélectionné des lectotypes pour les espèces déjà décrites. Nous avons pourvu pour chaque espèce des cartes de distribution, et nous avons illustré les organes génitaux mâles de même qu'un dessin général de l'espèce. L'*Ithytolus *ne comprend qu'une seule espèce:* C. orizabae. *Le sous-genre* Cyrtolaus *est composé de huit espèces:* C. lobipennis *Bates;* C. subiridescens *n. sp. (localité type 6.6 mi. n. Pueblo Nuevo, Chiapas);* C. brevispina *n. sp. (localité type Yerba Buena Mission, 1.5 mi.n. Pueblo Nuevo, Chiapas);* C. newtoni *n. sp. (localité type 22.4 mi. s. Valle Nacional, Oaxaca);* C. ricardo *n. sp. (localité type Volcan Tacaná, pres d'Union Juarez, Chiapas);* C. spinicauda *Bates;* C. furculifer *Bates; et* C. grumufer *n. sp. (localité type Yerba Buena Mission, 1.5 mi. n. Pueblo Nuevo, Chiapas). Les espèces vivent dans les forêts montagneuses. Nous avons pourvu*

une phylogénie reconstruite, avec la séquence des relations dans le même ordre que la liste ci-dessus. Nous proposons que le patron de distribution géographique et de différentiation morphologique est le resultat d'alternation de périodes d'isolation a l'intérieur et de périodes de dispersion entre les systèmes montagneux du Guatemala et du sud du Mexique.

Within the highly diverse and divergent carabid fauna of the Middle American Highlands the genus *Cyrtolaus* stands out both because of the distinctive and aesthetically appealing form of its members, and because of the uncertainties surrounding its origin and relationships. Together, we first encountered the genus near Pueblo Nuevo, Chiapas, on a hot, sunny day in August, 1965, when we took the only two specimens we saw of this group during a year of collecting in Mexico. We were impressed both by the peculiar appearance of these specimens, and by the seeming rarity of the genus to which they belonged. Subsequent study of type material in London and Paris exposed several interesting facts, the least important of which was that our specimens represented an undescribed species.

On subsequent trips, additional specimens were collected in the Pueblo Nuevo area, on the slopes of Volcan Tacaná, near the Pacific Coast and the southern border of Mexico, and in the Cuchumatanes Mountains of Guatemala. We also received important material from other persons. This provided sufficient material and the impetus for us to attempt an initial essay about *Cyrtolaus* including keys, descriptions and illustrations, and a classification based on what we believe to be its phylogenetic history. To locate the position of the genus within the Pterostichini, an important component of this study, we have had to review in a cursory fashion the classification of some of the major American elements of the tribe.

MATERIAL AND METHODS

Material. – This study is based on 70 adult beetles, including types of the four species previously described. Also, specimens were studied of all other pterostichine genera known from Middle America. In the text, museums and collections from which specimens were borrowed or in which types have been deposited are indicated by the following abbreviations:

BMNH	British Museum (Natural History), London, England;
CAS	California Academy of Sciences, San Francisco, California;
CNC	Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario;
FMNH	Field Museum of Natural History, Chicago, Illinois;
IPNM	Instituto Politecnico Nacional de Mexico, Mexico, D.F.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts;
MNHP	Museum National d'Histoire Naturelle, Paris, France;
UASM	Strickland Museum, Department of Entomology, University of Alberta, Edmonton, Canada;
USNM	National Museum of Natural History, Washington, D.C.

Methods. – In general, these are the same as described by us in previous works (Ball and Nègre, 1972; Whitehead, 1972), including our notions about definitions of species and higher taxa.

The following measurements were made because they seem to be useful in recognizing and studying affinities of the species. They were made with an ocular micrometer scale, in a binocular microscope.

The term "standardized body length" (SBL) in the descriptions is the sum of three measurements: length of head, measured on the left side from base of mandible to posterior margin of compound eye; length of pronotum along mid-line (P 1); and length of longer elytron from transverse basal line to apex (E 1).

Additional measurements taken and used to form ratios are: M 1 – length of left mandible, measured on dorsal surface from condyle to apex; Ant. art. 3 – length (l), measured from basal to apical margin; width (w), maximum linear transverse distance. Ratios are the following: M 1/P 1; P 1/E 1; ant. art. 3: w/l.

Descriptions are summaries of characters of adult beetles which are useful in species recognition. Character states shared by all or most of the species are listed in the description of the genus, and are not repeated in species descriptions. Illustrations were prepared with the aid of a *camera lucida* attached to a Wild M5 binocular microscope.

NOTES ABOUT STRUCTURE

A few details require some general explanation. Nomenclature of the parts of the mandibles (Fig. 2) is based on a system devised by Ball (1959). Appearance of the elongate slender mandibles with reduced teeth suggests that they might be used for reaching into confined spaces and for holding prey rather than for shearing. The reduced number and length of hairs associated with the ventral grooves also suggests a function for the mandibles different from that associated with the more generalized type of structure. Knowledge of feeding habits of these beetles would contribute much to understanding the function of the mandibles.

The endophallus of the male genitalia bears various sclerites and lobes. Because no general system of nomenclature is available for structures associated with the endophallus of pterostichines, we have chosen to designate the terminal sclerite on the basis of its form (c-shaped), to designate the spine-bearing sclerites by number, and to name one large lobe by its position– the "ventral lobe". See Figures 16 C and D for details. Descriptions are provided in conjunction with descriptions of the taxa.

RELATIONSHIPS AND CLASSIFICATION OF *CYRTOLAUS*

Bates (1882) described *Cyrtolaus* as a genus of Agonini, distinguished by modified mouthparts, but otherwise with agonine habitus. His discovery of a well developed elytral plica that crossed the epipleuron in a fourth species led him to erect the genus *Ithytolus,* and he placed it in the Pterostichini (1884). Because we regard *Ithytolus* and *Cyrtolaus* as congeneric, we must address first the question of the true relationships of this genus. This essay is of necessity preliminary and imprecise, because we cannot at this time state sister group relationships (Hennig, 1966).

Lindroth (1966) placed the Agonini and Pterostichini in one tribe, Pterostichini, represented in the New World by the subtribes Pterostichi, Synuchi, Sphodri, and Agoni. Ball and Nègre (1972) treated the Synuchi, Sphodri, and Old World Pristosiae as a monophyletic stock. (Mention was also made of the presumed sphodrine genera *Prosphodrus* and *Mexisphodrus;* Whitehead (1973) transferred *Mexisphodrus* to the Agonina, including it in the genus *Platynus).* If these three subtribes form a monophyletic stock, then how is this stock related to the Agonina and Pterostichina? Traditionally, the Agonina have been considered a phylogenetically derived group, and the Pterostichina have been regarded as a much older group. This idea may be incorrect. Overall habitus or body plan of the Agonina is generalized, and is approximated in diverse groups of other carabids: e.g., in various tribes of styliferous genera; in some of the less derived Truncatipennes, such as the Tribe Perigonini (a placement suggested by T. L. Erwin

in litt.); and in the harpaline subtribe Bradycellina. In carabid beetles, the male genitalia are rotated 90°; if the position is asymmetric, one would expect asymmetry to develop in structure, and it has done so in many carabid lineages; one would further expect the asymmetry to be progressive, not regressive. In the Pterostichini, asymmetry in form of the median lobe and especially of the parameres is slight in Agonina, more pronounced in Pterostichina, and moderate to relatively extreme in Synuchina, Sphodrina and Pristosiina. Exceptions may be expected, but in the direction of greater asymmetry, examples of which are the styloid right paramere of *Abacidus* (see Lindroth, 1966: 536), *Percolaus* (T. L. Erwin, *in litt.*), *Refonia* and *Feronina*, all members of the Pterostichina. Also, the presence of distal setae on the parameres, known in the genera *Sericoda* and *Elliptoleus* (Whitehead, 1973) of the Agonina, but not in other Pterostichini, is more likely an ancestral condition than a secondarily derived one. These conclusions suggest that the Agonina may be more closely related to the Pterostichina rather than to other groups of Pterostichini, and form the basis for a partial resolution of the dilemma faced by Bates concerning relationships of *Cyrtolaus* and *Ithytolus*.

In a study of Mexican *Platynus* (Whitehead, 1973), *Cyrtolaus* was treated as a genus of Agonina. We subsequently found that the male genitalia of *Cyrtolaus* have undergone a reversal in symmetry and lie on the left side rather than the right as in most Pterostichini, and that the left paramere of *Cyrtolaus* is small and slender as typical of the right paramere of most Pterostichina. The only other pterostichine genera with reversed symmetry are *Calathus* (subgenus *Tachalus*) and *Pristosia*, both with the left paramere styloid (Ball and Nègre, 1972).

Other characters that may bear on the phylogenetic placement of *Cyrtolaus* concern the supraorbital setae of the head, form of tarsal article 4, ventral adhesive vestiture of the male front tarsus, form of the elytral plica, number and position of anal setae, and structures of the male endophallus.

The number of supraorbital setae in carabids is in most groups constant and is important in diagnoses of many of the higher carabid tribes. In the Pterostichini, there normally are two pairs. No exceptions are known in the Synuchina or Sphodrina. In the Pterostichina, at least in the New World, only one species, *Pterostichus (Gastrellarius) honestus*, has only one pair of supraorbital setae. In the Agonina, however, various Old and New World tropical species of *Platynus* and *"Colpodes"* have but one pair (Darlington, 1952; Whitehead, 1973). Against this background, the fact that some species of *Cyrtolaus* have one pair of supraorbital setae—a derived character state—suggests a character instability of phylogenetic significance: perhaps *Cyrtolaus* and *Platynus* share a stem relationship.

The characteristic "article 4 of tarsus bilobed" is shared by members of *Cyrtolaus* and many tropical members of the subtribe Agonina. As above, this is probably not synapotypy, but the ability to develop this character may be indicative of relationship.

Absence of adhesive vestiture from the ventral surfaces of the front tarsi of males is unusual among both Pterostichina and Agonina. However, males of *Percolaus championi* Bates are without vestiture, and the front tarsomeres are as narrow as are the tarsomeres of the middle and hind legs.

Among the Pterostichina, the elytral epipleura are crossed by a plica that is visible externally, while in the Agonina they are not. Exceptions in the Pterostichina are few, notably in some species of *Loxandrus* and *Pterostichus* (subgenera *Cryobius* and *Lyperopherus*) and in the genus *Percolaus*. In some species of *Cyrtolaus*, the elytral epipleura are not crossed. As with the supraorbital setae, this character instability may have some phylogenetic significance: it suggests a placement of *Cyrtolaus* near the base of the Pterostichina—but outside the Agonina.

Among both the Pterostichina and Agonina, the numbers of anal setae are usually two in the males and four in the females. However, many species of tropical American *Platynus* exhibit increased numbers: four among males and six to eight among females. This is also true of the

members of *Cyrtolaus*, and again, the ability to develop this character state may be indicative of relationship.

The male endophallus in many species of the agonine genera *Platynus* and *Onypterygia* is elongate, armed with one or more basal and median spinose sclerites—probably a plesiotypic character state. Similar sclerites are developed in *Cyrtolaus,* and not in other pterostichoids. Presence of these sclerites is regarded as apotypic in *Cyrtolaus*, and hence they are regarded as having developed in parallel with similar sclerites in the Agonina—another instance of supposed relationship based on ability to develop a particular character state.

If we do not know the sister group of *Cyrtolaus*, where should we look for it? One possibility implied in the above discussion is that all the rest of the Pterostichina together may form the sister group. Another possibility is suggested by the evident great age of *Cyrtolaus* (as suggested by T. L. Erwin *in litt.,* the fused elytra of most of the species indicate both antiquity and long-term residence in Central America): relationships may be with some Old World, especially Oriental, groups, and may antedate continental drift. For the present, we choose to exclude *Cyrtolaus* from both the Agonina and Pterostichina, and propose here a new subtribe for its reception, the Cyrtolaina, defined below.

To round out this survey, we list here the subtribes of Pterostichini that we recognize for the New World: Agonina; Lachnophorina; Cyrtolaina; Euchroina; Myadina; Stomina (one Palaearctic genus, one species introduced into the New World); Pterostichina; Synuchina; Sphodrina; Pristosiina; Antarctiina; and Cratocerina. Many of the South American genera presently included in the Pterostichina will probably have to be removed to one or more subtribes of their own. With Reichardt (1973: 323-326) we agree that *Catapiesis* Solier and *Homalomopha* Brullé are not pterostichines, and must be placed in a tribe of their own.

THE SUBTRIBE CYRTOLAINA, NEW SUBTRIBE

Diagnostic combination. – Body bulky, cychroid, integument glabrous except few fixed setae. Antennae with articles 1-3 glabrous, except single seta or apical ring of long setae. Mouthparts (mandibles, maxillae and labial palpi) elongate (Figs. 2, 3 and 5); mandibles with reduced teeth, molar absent, ventral groove (Fig. 2C) very shallow, with large punctures, each puncture with very short setae; maxilla, article 2 thickened, basal article of galea much longer than apical article (Fig. 3); labium, mentum with simple median tooth, and with pair of pores posterior to mental setae. Prosternum, intercoxal process ridged at apex ("lipped"). Metathorax reduced, metepisternum with anterior and lateral margins subequal in length. Tarsal articles 1-4 strigulose dorsally, article 4 bilobed, with outer lobe subequal in length to basal part of article, and longer than inner lobe; article 5 smooth dorsally, asetose ventrally. Elytra fused in mid-line, or not, striate, striae 2 and 3 joined at base, laterad of basal setigerous puncture. Hind wings tiny stubs. Male genitalia, median lobe in repose on left side, left paramere reduced, right paramere larger, conchoid. Endophallus with apical C-sclerite, as in Fig. 14A, with or without spinose sclerites more basal in position.

This group contains the single genus *Cyrtolaus* Bates, confined, insofar as known, to wet tropical mountain forests of Guatemala and Mexico.

Genus *Cyrtolaus* Bates, 1882

The taxa of Pterostichini with which members of *Cyrtolaus* might be confused, or which have brachypterous members within the geographical range of this genus are subgenus *Platynella* Casey (genus *Platynus*), *Percolaus* Bates, *Dyschromus* Chaudoir, and subgenus *Allotriopus* Bates (genus *Pterostichus*). The subgenus *Platynella* shares with *Cyrtolaus*

strigulose tarsomeres 1-4, but members of the two groups are readily distinguished from one another by differences in form of the prosternal intercoxal process (lipped in *Cyrtolaus*, flat in *Platynella*), in form of the maxillary palpus (article 2 swollen, relatively short in *Cyrtolaus* (Fig. 3), in *Platynella* not swollen and relatively longer), and in form of mental tooth (apex not shallowly notched in *Cyrtolaus*, notched in *Platynella*). Strigulose tarsomeres, simple mental tooth, short thick article 2 of the maxillary palpus and lipped intercoxal process separate members of *Cyrtolaus* from those of *Percolaus*, *Evarthrus*, and subgenera *Allotriopus* and *Ophryogaster*. The members of *Dyschromus* are readily distinguished by metallic color of the dorsal surface, flat prosternal intercoxal process, securiform terminal articles of labial palpi, and tarsomere 5 with ventro-lateral setae.

Description. – Form cychroid (Fig. 6A-13A). Standardized body length 9.0-15.0 mm.

Color. Body black. Mandibles infuscated. Remaining mouthparts, antennae and legs rufous.

Microsculpture. Head, dorsum, microsculpture meshes small, isodiametric, lines fine; ventral surface, meshes transverse, lines fine to obsolescent. Pronotum, meshes transverse, narrow, lines finer than on dorsum of head. Thoracic sterna and pleura, meshes transverse, narrow, generally wider than pronotal meshes. Elytra, meshes isodiametric or transverse. Abdominal sterna, meshes transverse medially, approximately isodiametric laterally.

Luster. Body generally shining, with pronotum faintly iridescent; elytra iridescent or not.

Head. Supraorbital setae 1 or 2 pairs. Dorsum with elongate, narrow frontal impressions. Clypeus with single pair setae. Eyes small, tempora slightly swollen. Antennae average, articles 1-4 without covering of short setae.

Mouthparts. Labrum (Fig. 1) approximately rectangular, anterior margin shallowly concave, dorsal setae remote from anterior margin, lateral pair longer than medial pair. Mandibles (Fig. 2) elongate, terebrae slender; left mandible (Fig. 2A, 2C) with terebral margin laterad of retinacular ridge, latter cutting edge; terebral tooth small, in basal third; posterior retinacular tooth small, ventrally represented by short ridge; premolar tooth small, premolar margin glabrous; ventral groove (Fig. 2C) very shallow, with series of punctures, each with one or more short setae. Right mandible (Fig. 2B, 2D) like left, but differing in detail–cutting edge, terebral margin, terebral tooth larger, retinacular tooth better developed dorsally, less developed ventrally. Maxillae elongate (Fig. 3) generally as in average pterostichines; stipes and palpifer each with lateral seta; galea with first article about 4 times longer than terminal article; maxillary palpus with article 2 thickened, article 3 elongate. Labium with submentum quadrisetose; mentum (Fig. 4) with anterior margin shallowly concave, lateral lobes acute apically, median tooth simple, prominent; epilobes well developed; ventral surface with seta and small pore each side of mid-line; ligula (Fig. 5) broad, apical margin bisetose, emarginate apically; paraglossae (Fig. 5) each narrow membranous lobe; labial palpus (Fig. 5) with articles 2 and 3 elongate, article 2 bisetose.

Thorax. Pronotum various in form, wider than long; anterior margin truncate to slightly excised; posterior margin truncate to bi- or tri-sinuate; lateral margins rounded, sinuate or not posteriorly; anterior angles narrowly rounded, slightly projected anteriorly or not; posterior angles broadly rounded to acute. Disc slightly convex, postero-laterally more sharply declivous than antero-laterally; sides more or less explanate and elevated posteriorly; median longitudinal and posterior transverse impressions clearly indicated, anterior transverse impression shallow, faintly indicated; lateral grooves distinct; posterior-lateral impressions linear, deep posteriorly, extended forward each side mediad of lateral grooves. Prosternum with apex of intercoxal process with prominent ridge ventrally ("lipped"). Metathorax reduced, metepisternum with lateral and anterior margins subequal in length.

Hind wings. Reduced to stubs subequal in length to metatergum.

Legs. As in Fig. 6A-13A, average for Pterostichini. Hind femur without preapical setae. Tarsi with articles flattened dorsally, articles 1-4 strigulose dorsally, article 5 with dorsum smooth, ventrally without setae; article 4 distinctly, asymmetrically lobed, outer lobe at least as long as basal part of article; fore tarsus of male not or very narrowly expanded, without adhesive vestiture ventrally, or with vestiture confined to articles 1 and 2.

Elytra. As in Fig. 6A-13A, elongate, fused in mid-line or not. Humeri more or less constricted. lateral margins more or less rounded, slightly to markedly sinuate postero-laterally; apex more or less distinctly spined; more or less markedly convex, distinctly vaulted in some species (Fig. 6B-13B); basal ridge sinuate, extended from humeral angle to scutellum. Striae moderately deep, finely or coarsely punctate; striae 1 and 2 joined at base, laterad of basal setigerous puncture. Intervals slightly convex to costate; interval 3 with single setigerous puncture near middle.

Abdomen. Anal setae 2 or 4 in male. 4 or 6-8 in females.

Male genitalia. Median lobe as in Fig. 14A, on right side in repose; sclerotized completely ventrally, dorsally sclerotization extended from base to apical half; apical orifice dorsal in position; apical portion short and narrow (Fig. 14B) to broad and moderately elongate (Fig. 20B). Parameres pterostichoid, right one larger than left. Endophallus membranous with apical curved sclerite (c-sclerite) and with or without spinose sclerites 1-3, and with or without ventral membranous lobe distally (Fig. 16C, D to 20C).

Ovipositor and female genitalia. Not studied in detail.

Notes on habitat. – All specimens for which we have data were collected on the ground or in logs in mountain forests, at elevations in excess of 5000 feet above sea level. The forests

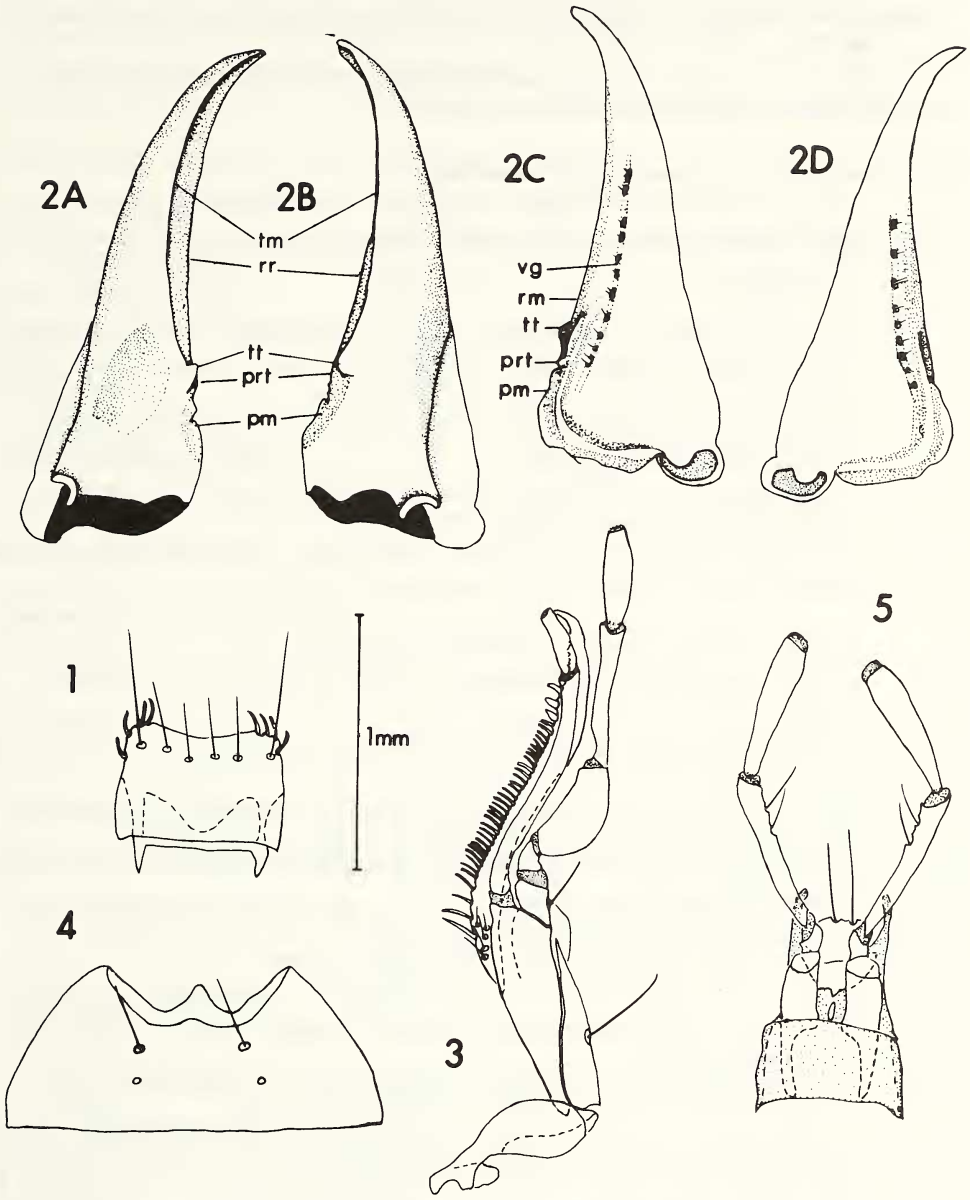


Fig. 1-5. Mouthparts of *Cyrtolaus ricardo*, new species (Volcan Tacaná, Chiapas). Fig. 1. Labrum, dorsal aspect. Fig. 2. Mandibles: A and B, left and right, respectively, tm - terebral margin, rr - retinacular ridge, tt - terebral tooth, prt - posterior retinacular tooth, pm - premolar area; C and D, ventral aspect, left and right, respectively, vg - ventral groove, other abbreviations as for dorsal aspect. Fig. 3. left maxilla, ventral aspect. Fig. 4. mentum, ventral aspect. Fig. 5. prementum and palpi, ventral aspect.

were of several different types: wet, sweet gum–pine–oak; tropical montane forest; or tropical cloud forest (the tropical mountain forest occurring above at least the lower part of the conifer zone).

Geographical distribution. – The species are known from southern Mexico and Guatemala (Fig. 22 and 23).

Classification. – The nine species included in this genus are distributed between two subgenera: *Ithytolus* and *Cyrtolaus (sensu stricto).*

Key to the subgenera and species of *Cyrtolaus* Bates

1 Pronotum with anterior marginal bead complete, posterior lateral setae near hind angles; elytron with plica well developed, epipleuron interrupted ("crossed"), striae impunctate; anal setae 2 in male, 4 in female ..... Subgenus *Ithytolus* Bates ..... *C. orizabae* (Bates), p. 600

1' Pronotum without anterior marginal bead, posterior lateral setae distinctly anterad of hind angles; elytral epipleuron interrupted or not, striae punctate; anal setae 4 in male, 6 to 8 in female ..... Subgenus *Cyrtolaus* 2

2 (1) Elytron with epipleuron interrupted, striae distinctly punctate at apex only; labrum with four marginal setae ..... *C. lobipennis* Bates, p. 607

2' Elytral epipleuron not interrupted, plica on ventral surface of elytron, only; striae distinctly punctate throughout their length 3

3 (2) Elytron with microsculpture of dense transverse lines, luster faintly iridescent; striae grossly punctate, intervals carinate; apex spined or not ..... *C. subiridescens,* new species, p. 607

3' Elytron with microsculpture isodiametric, apex spined 4

4 (3) Elytron with interval 2 swollen apically; head with single pair of supraorbital setae 5

4' Elytron with interval 2 not swollen and raised apically; supraorbital setae 4 (2 pairs) or 3 6

5 (4) Elytron with interval 3 strongly raised apically; disc of pronotum with microsculpture normal, surface shining, without sericeous luster ..... *C. furculifer* Bates, p. 611

5' Elytral interval 3 not raised apically; disc of pronotum with lines of microsculpture dense, surface with sericeous luster ..... *C. grumufer,* new species, p. 612

6 (5) Pronotum with anterior angles produced (Fig. 9A), hind angles rounded, lobate; elytra strongly vaulted (Fig. 9B), striae grossly punctate ..... *C. spinicauda* Bates, p. 610

6' Pronotum with anterior angles not produced, elytra not vaulted (Fig. 10B, 11B), striae finely punctate 7

7 (6') Elytron with apical spine long (Fig. 10A), apical declivity gradual (Fig. 10B) ..... *C. ricardo*, new species, p. 609

7' Elytron with apical spine short (Fig. 10D, 11A), apical declivity gradual or abrupt (Fig. 11B) 8

8 (7') Pronotum with posterior angles acute, striae of elytra very obscurely punctate anteriorly, apical declivity more gradually sloped ..... *C. newtoni,* new species, p. 609

8' Pronotum with posterior angles rectangular, striae distinctly punctate anteriorly, slope of apical declivity more abrupt ..... *C. brevispina,* new species, p. 608

Subgenus *Ithytolus* Bates, 1884

Ithytolus Bates, 1884: 278. Species originally included: *I. anomalus* Bates, 1884, and *Cyrtolaus*

lobipennis Bates, 1882. TYPE SPECIES (here designated): *Ithytolus anomalus* Bates, 1884: 278.

Pterostichus (Ithytolus); Csiki, 1930: 585.

The character states indicated in the key plus details of structure of elytra and male genitalia presented below, in the description of the single included species, are sufficient to distinguish *Ithytolus* from *Cyrtolaus (sensu stricto)*.

Geographical distribution. – This group is known only from Orizaba, Veracruz (Fig. 22).

Table 1. Data on Variation in Standardized Body Length (SBL) (in mm) among the Species of *Cyrtolaus* Bates.

Species Name	Males N	Range	Mean	Females N	Range	Mean
C. orizabae	2	9.0 - 9.7	9.35			
C. lobipennis	1	11.8				
C. subiridescens						
Pueblo Nuevo	2	10.7 - 11.3	11.00	2	10.5 - 10.6	10.55
Tenejapa	3	10.7 - 11.4	10.90	5	10.6 - 11.3	10.96
Cuchumat. Mts.	7	10.5 - 11.3	10.98	7	10.6 - 11.6	11.06
C. spinicauda	1	11.5		1	12.4	
C. newtoni				1	9.8	
C. ricardo	15	10.3 - 11.9	10.91	6	10.9 - 11.6	11.15
C. brevispina	1	12.8				
C. furculifer				3	11.6 - 13.3	12.27
C. grumufer	4	13.5 - 15.0	14.00	2	13.0 - 14.3	13.65

Table 2. Data on Variation in the Ratio M 1/P 1 among the Species of *Cyrtolaus* Bates.

Species Name	Males N	Range	Mean	Females N	Range	Mean
C. orizabae	2	0.54 - 0.60	0.57			
C. lobipennis	1	0.67				
C. subiridescens						
Pueblo Nuevo	2	0.61 - 0.66	0.64	2	0.68 - 0.71	0.70
Tenejapa	3	0.60 - 0.67	0.64	5	0.65 - 0.69	0.67
Cuchumat. Mts.	7	0.66 - 0.71	0.69	7	0.69 - 0.71	0.70
C. spinicauda	1	0.68		1	0.68	
C. newtoni				1	0.60	
C. ricardo	15	0.63 - 0.73	0.69	6	0.64 - 0.72	0.69
C. brevispina	1	0.61				
C. furculifer				3	0.58 - 0.64	0.60
C. grumufer	4	0.56 - 0.58	0.57	2	0.55 - 0.60	0.58

Table 3. Data on Variation in the Ratio P 1/E 1 among the Species of *Cyrtolaus* Bates.

Species Name	Males N	Males Range	Males Mean	Females N	Females Range	Females Mean
C. orizabae	2	0.45 - 0.47	0.46			
C. lobipennis	1	0.44				
C. subiridescens						
Pueblo Nuevo	2	0.44	0.44	2	0.42	0.42
Tenejapa	3	0.43 - 0.46	0.45	5	0.41 - 0.42	0.416
Cuchumat. Mts.	7	0.36 - 0.42	0.39	7	0.37 - 0.40	0.39
C. spinicauda	2	0.43		1	0.39	
C. newtoni				1	0.45	
C. ricardo	15	0.38 - 0.43	0.40	6	0.38 - 0.41	0.40
C. brevispina	1	0.46				
C. furculifer				3	0.41 - 0.43	0.42
C. grumufer	4	0.46 - 0.51	0.48	2	0.48	0.48

Table 4. Data on Variation in the Ratio Ant. Art. 3 w/l among the Species of *Cyrtolaus* Bates.

Species Name	Males N	Males Range	Males Mean	Females N	Females Range	Females Mean
C. orizabae	2	0.41 - 0.47	0.44			
C. lobipennis	1	0.45				
C. subiridescens						
Pueblo Nuevo	2	0.29	0.29	2	0.32 - 0.33	0.325
Tenejapa	3	0.28 - 0.32	0.29	5	0.29 - 0.33	0.31
Cuchumat. Mts.	7	0.24 - 0.35	0.31	7	0.37 - 0.40	0.39
C. spinicauda	1	0.28				
C. newtoni				1	0.37	
C. ricardo	15	0.26 - 0.32	0.30	6	0.29 - 0.32	0.30
C. brevispina	1	0.38				
C. furculifer				3	0.20 - 0.32	0.31
C. grumufer	4	0.30 - 0.36	0.33	2	0.32	0.32

Cyrtolaus (Ithytolus) orizabae (Csiki, 1930)

Ithytolus anomalus Bates, 1884: 278. LECTOTYPE male (here selected), labelled: Orizaba [handwritten]; H. W. Bates Biol. Cent. Amer; Ithytolus anomalus Bates [handwritten]; LECTOTYPE [red paper]; (MNHP). PARALECTOTYPE male, labelled: Type H.T. [circle, bordered in red]; Mexico Salle Coll.; Sp. figured; BCA Col. I. 1. Ithytolus anomalus Bates; Ithytolus anomalus Bates [handwritten] (BMNH). TYPE LOCALITY: Orizaba, Veracruz.

Pterostichus (Ithytolus) orizabae Csiki, 1930: 585. New combination and new name for *Pterostichus (Ithytolus) anomalus* Bates, 1884, not *P. (Ophryogaster) anomalus* Chaudoir, 1878. TYPE LOCALITY. – Orizaba, Mexico.

Note on synonymy. – When this species was transferred to *Pterostichus,* Csiki renamed it

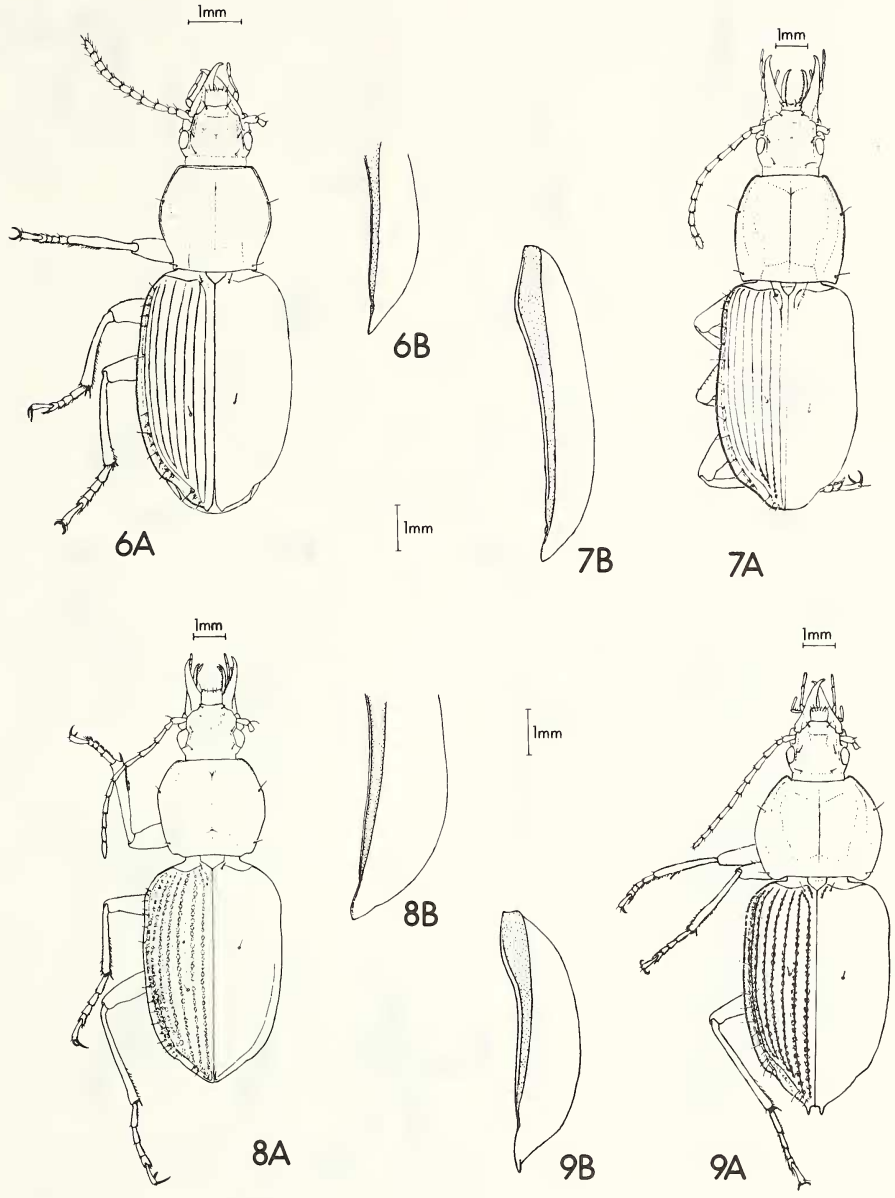


Fig. 6. *Cyrtolaus orizabae* Csiki (Orizaba, Veracruz, MNHP); A, male, dorsal surface; B, left elytron, lateral aspect. Fig. 7. *Cyrtolaus lobipennis* Bates (San Geronimo, Guatemala, BMNH); A, male, dorsal aspect; B, left elytron, lateral aspect. Fig. 8. *Cyrtolaus subiridescens*, new species (6.6 mi. n. Pueblo Nuevo, Chiapas, USNM); A, male, dorsal aspect; B, left elytron, lateral aspect. Fig. 9. *Cyrtolaus spinicauda* Bates (59.5 kil. s. Coban, Guatemala, USNM); A, dorsal aspect; B, left elytron, lateral aspect.

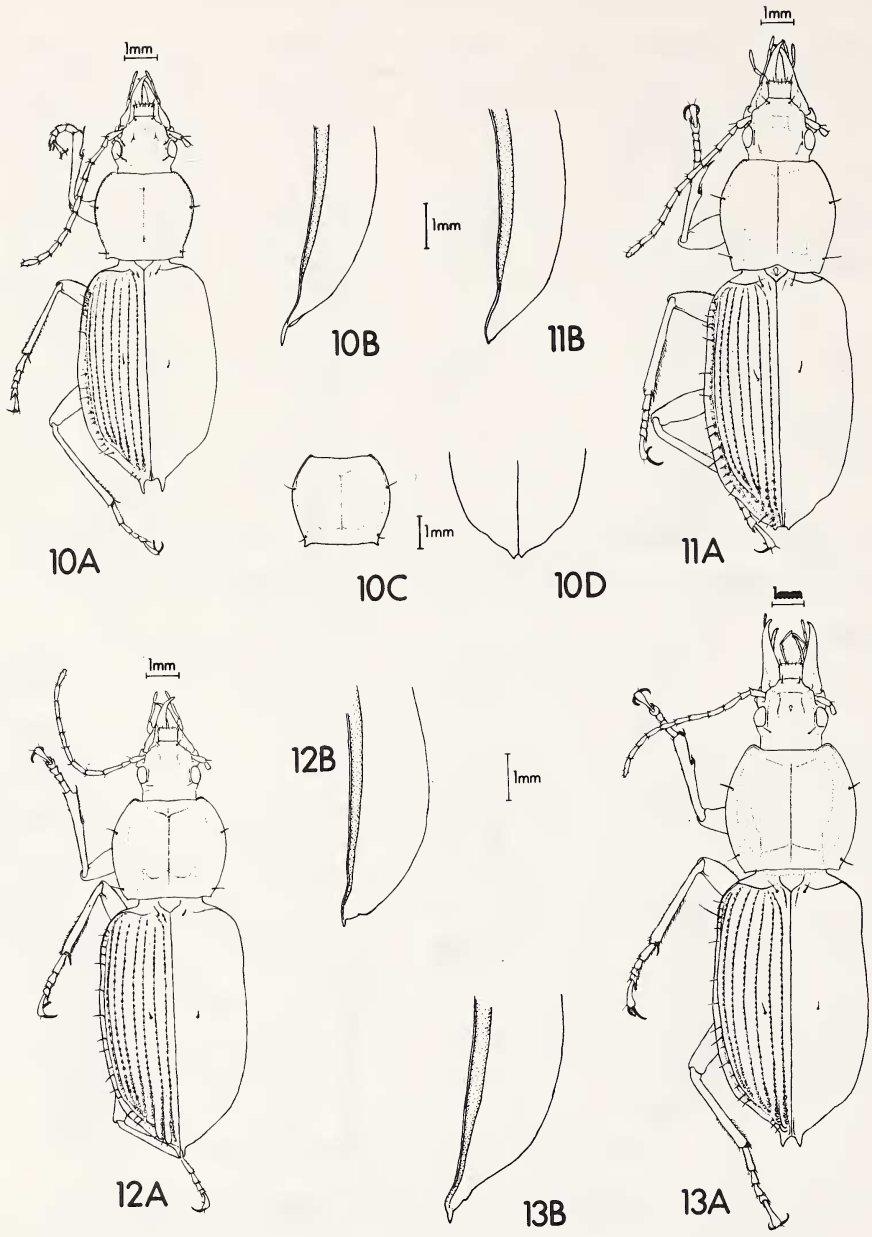


Fig. 10. *Cyrtolaus ricardo*, new species (Volcan Tacaná, Chiapas, USNM); A, male, dorsal aspect; B, left elytron, lateral aspect. Fig. 10C and D. *Cyrtolaus newtoni*, new species; C, pronotum, dorsal aspect; D, elytral apices, dorsal aspect. Fig. 11. *Cyrtolaus brevispina*, new species (Yerba Buena Mission, 1.5 mi. n. Pueblo Nuevo, Chiapas, USNM); A, male, dorsal aspect; B, left elytron, lateral aspect. Fig. 12. *Cyrtolaus furculifer* Bates (Barranca Providencia, Volcan Tacaná, Union Juarez, Chiapas, UASM); A, female, dorsal aspect; B, left elytron, lateral aspect. Fig. 13. *Cyrtolaus grumufer,* new species (Yerba Buena Mission, 1.5 mi. n. Pueblo Nuevo, Chiapas, USNM); A, male, dorsal aspect; B, left elytron, lateral aspect.

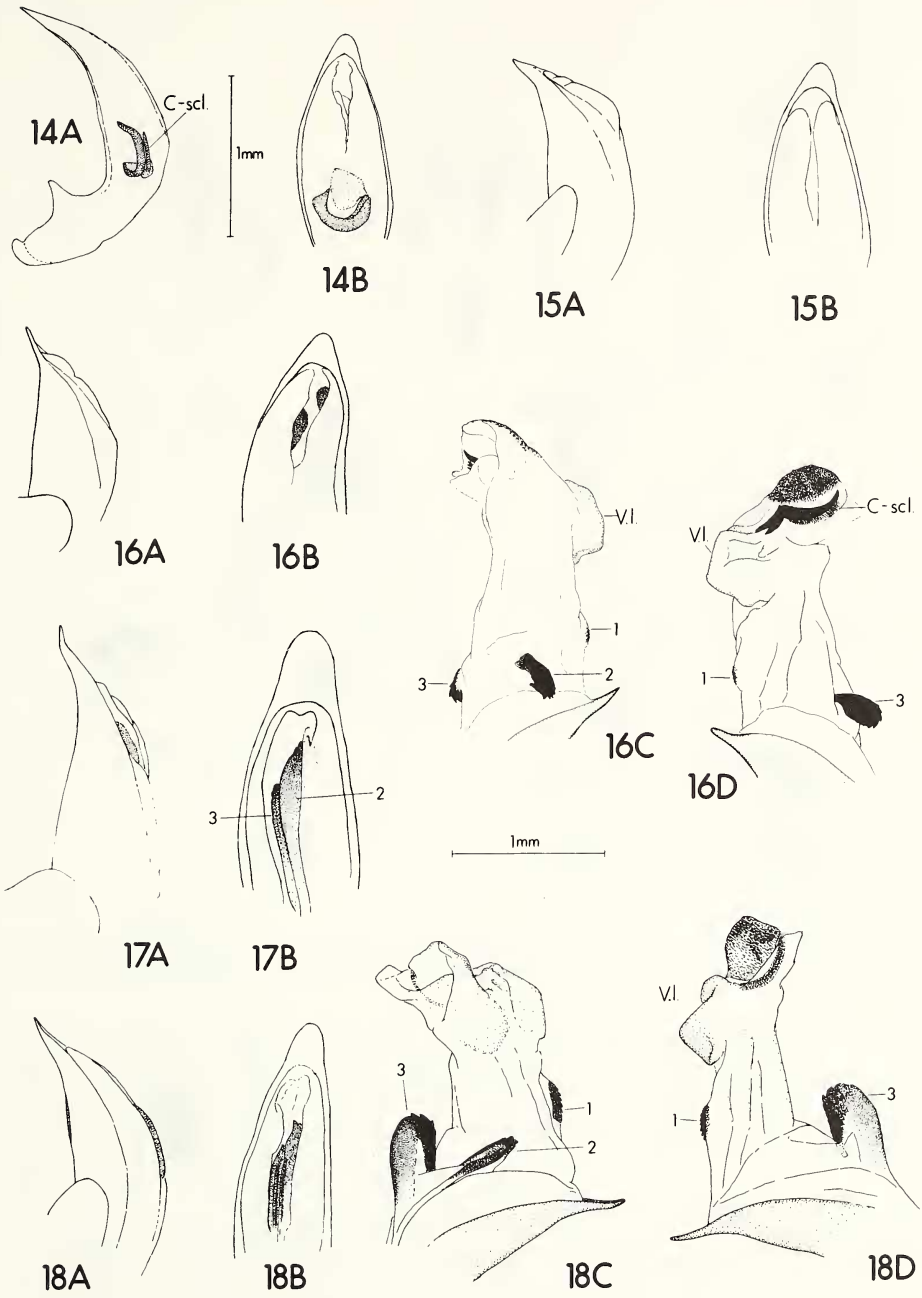


Fig. 14-18. Male genitalia. Fig. 14. *Cyrtolaus orizabae* Csiki: A, median lobe, right lateral aspect; B, median lobe, apical portion, dorsal aspect. Fig. 15. *Cyrtolaus lobipennis* Bates: A, median lobe, apical half, right lateral aspect; B, median lobe, apical half, dorsal aspect. Fig. 16. *Cyrtolaus subiridescens,* new species: A, median lobe, apical half, right lateral aspect; B, median lobe, apical half, dorsal aspect; C, endophallus everted, left lateral aspect; D, endophallus everted, right lateral aspect; C - scl. - C-sclerite; 1, 2 and 3 - spinous sclerites 1, 2 and 3, respectively; V.I. - ventral lobe. Fig. 17. *Cyrtolaus spinicauda* Bates (Purula, Guatemala, BMNH): A, median lobe, apical half, right lateral aspect; B, median lobe, apical half, dorsal aspect; 2, 3-spinous sclerites 2 and 3, respectively. Fig. 18. *Cyrtolaus ricardo*, new species: A, median lobe, apical half, right lateral aspect; B, median lobe, apical half, dorsal aspect; C, endophallus everted, left lateral aspect; B, endophallus everted, right lateral aspect; lettering as for Fig. 16C and D.

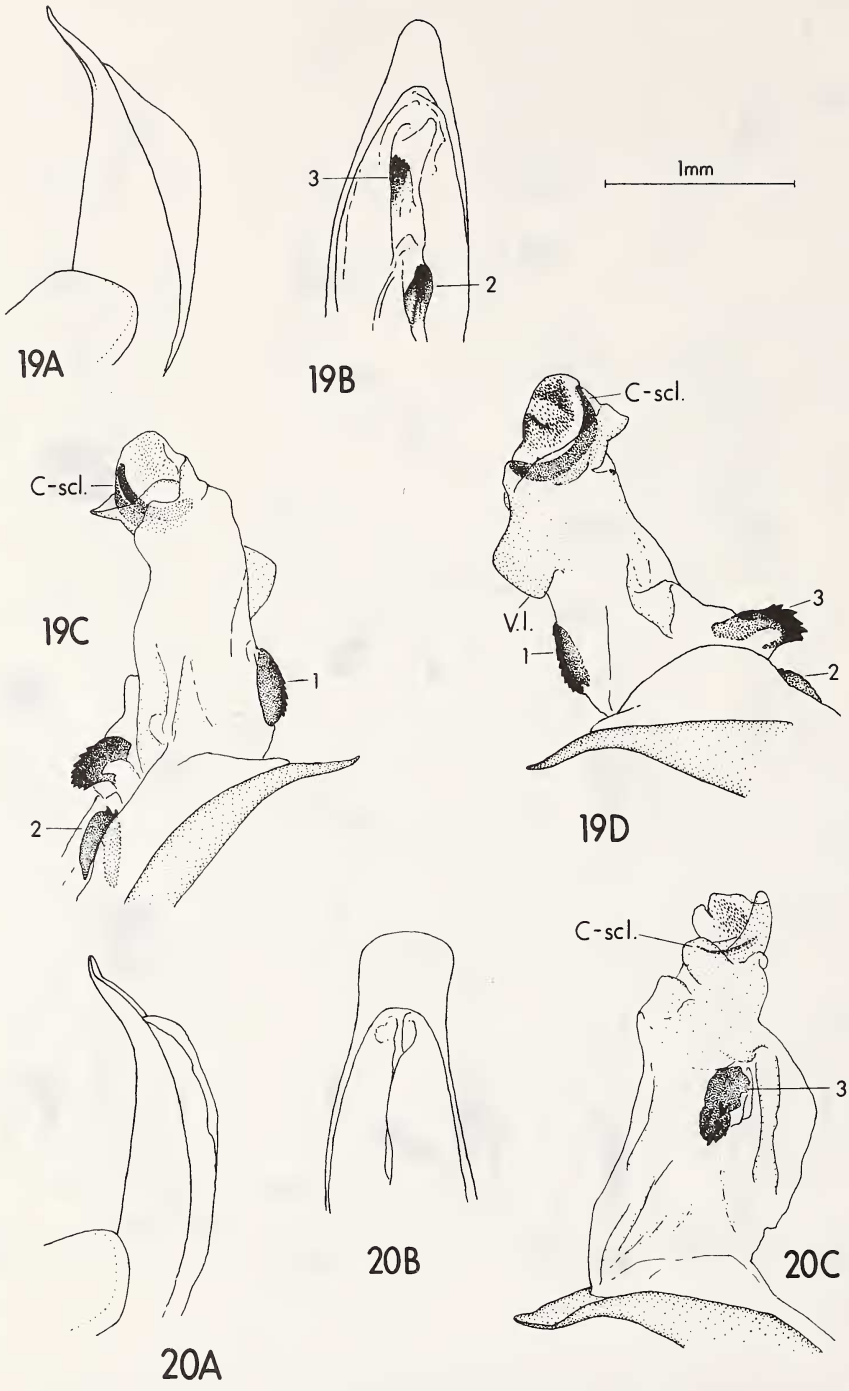


Fig. 19. *Cyrtolaus brevispina*, new species: A, median lobe apical half, right lateral aspect; B, median lobe, apical half, dorsal aspect; C and D, endophallus everted, left and right aspects, respectively; lettering as for Fig. 16C and D. Fig. 20. *Cyrtolaus grumufer*, new species: A, median lobe, apical 3/4, right lateral aspect; B, median lobe, apical 1/3 dorsal aspect; C, endophallus, everted, right lateral aspect; symbols as for Fig. 16C and D.

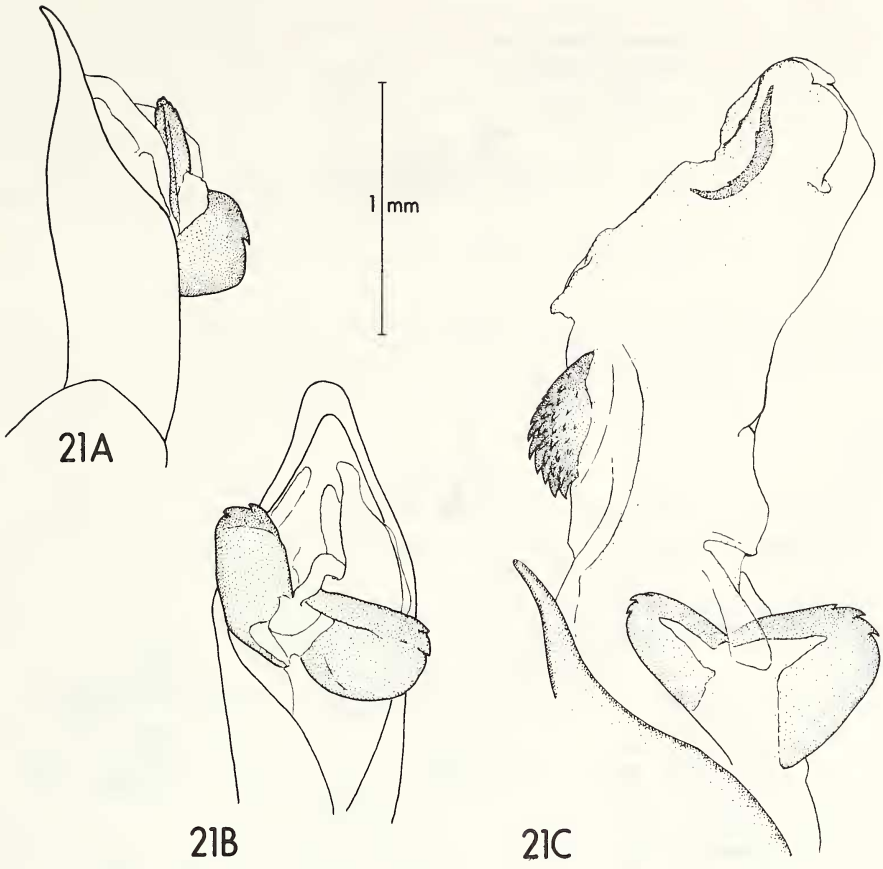


Fig. 21. *Cyrtolaus furculifer* Bates (Cerro Zunil, Guatemala): A, median lobe, left lateral aspect; B, median lobe, apical half, dorsal aspect; C, endophallus everted, right lateral aspect.

because *P. anomalus* Bates, 1884 became a secondary junior homonym of *P. anomalus* Chaudoir, 1878. Transfer of the Bates species from *Pterostichus* to *Cyrtolaus* eliminates the homonymy. Had the replacement name *P. orizabae* Csiki been proposed after 1960, it would be necessary to revert to the epithet *anomalus* for the Bates species (International Code of Zoological Nomenclature, Article 59 (c), 1964). However, as the former name was proposed prior to 1960, it is retained as the specific epithet for this species.

Diagnostic characteristics are presented in the key and in the subgeneric characterization.

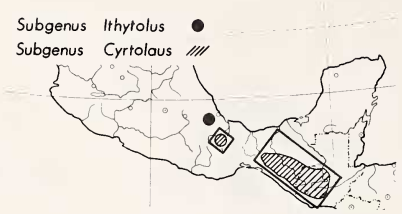
Description. – Form as in Fig. 6A. Size small for genus. Antennal and tarsal articles short. For data on standardized body length, and ratios M 1/P 1, P 1/E 1, and Ant. Art. 3 w/1, see Tables 1 to 4. For data on variation in the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture meshes fine, those of elytra isodiametric. Dorsal surface shining. Supraorbital setigerous punctures two pairs.

Pronotum as in Fig. 6A, anterior margin beaded, hind angles acute. Fore tarsus of male not expanded, without adhesive vestiture. Elytra dehiscent, form as in Fig. 6A and B, moderately vaulted; lateral margin moderately sinuate preapically. Humerus with small tooth; plica visible laterally, epipleuron interrupted; intervals slightly convex.

Male genitalia with median lobe as in Fig. 14A and B; apical portion not sinuate (lateral aspect), short narrowly rounded (dorsal aspect). Endophallus with C-sclerite, only.

Geographical affinities. – The range of *C. orizabae* is isolated from that of all other species. of the genus.



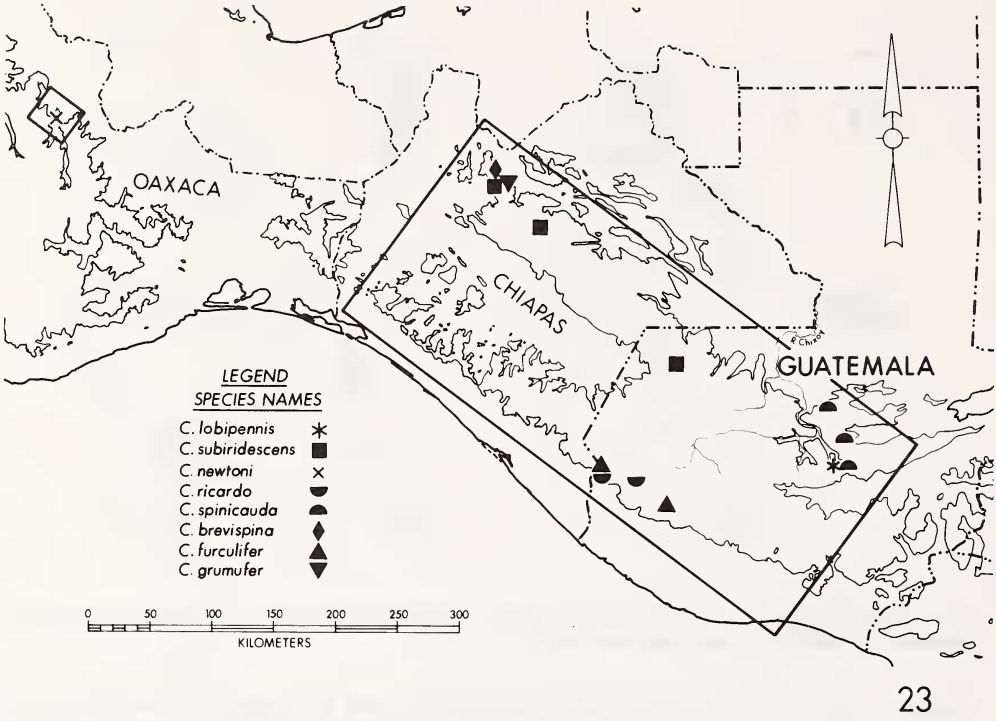


Fig. 22. Map of southern portions of Mexico and Guatemala, illustrating generalized ranges of subgenera of *Cyrtolaus* Bates.
Fig. 23. Map of southern Mexico and Guatemala, illustrating positions of localities for the species of subgenus *Cyrtolaus*.

Relationships. – This species is closest to *C. lobipennis* Bates, although many of the shared character states are probably the result of parallelism or convergence.

Material examined. – The type specimens, only, both collected near Orizaba, Veracruz.

Subgenus *Cyrtolaus (sensu stricto)*

Cyrtolaus Bates, 1882: 99. Species originally included: *C. furculifer* Bates, 1882, *C. spinicauda* Bates, 1882, and *C. lobipennis* Bates, 1882. TYPE SPECIES: *C. furculifer* Bates, 1882, (subsequent designation, by Kirby, 1883:32). –Csiki, 1931: 766. Whitehead, 1973: 175.

In addition to characteristics presented in the key, this group is distinguished from *Ithytolus* by the elytra being fused, not dehiscent, by a tendency for the pronotum to increase disproportionately in length as size increases (Fig. 24), and by generally larger size of its members (Table 1).

Except for the members of *C. lobipennis* Bates, the species of *Cyrtolaus (sensu stricto)* exhibit the following features in common: internal plica not interrupting the elytral epipleuron, not visible laterally, confined to ventral surface of the elytron; antennal (Table 4) and tarsal articles more elongate; males with articles 1 and 2 ventrally with adhesive vestiture; internal sac with spinose sclerites.

Geographical distribution. – The 8 species included in this subgenus are known only from the Guatemalan, Chiapan, and Oaxacan Highlands (Fig. 22 and 23).

Cyrtolaus (sensu stricto) lobipennis Bates, 1882

Cyrtolaus lobipennis Bates, 1882: 100. HOLOTYPE Male, labelled: TYPE H.T. [circular label, ringed in red]; Santa Cruz [handwritten]; S. Geronimo Guatemala Champion; BCA Col. I. 1. Ithytolus lobipennis Bates; Cyrtolaus lobipennis Bates [handwritten]. (BMNH). TYPE LOCALITY: San Geronimo, Guatemala.

Ithytolus lobipennis; Bates, 1884: 278.

Pterostichus lobipennis; Csiki, 1930: 585.

In addition to the character states presented in the key, members of this species are distinguished by relatively short antennae and tarsi, and by the pronotum with sides not sinuate posteriorly, not broadly rounded, and base relatively broad. Males are distinguished from those of the other species of this subgenus by lack of adhesive vestiture on the ventral surfaces of fore tarsal articles 1 and 2, and by lack of spinose sclerites from the internal sac of the male genitalia.

Description. – Body form as in Fig. 7A. Size large for genus, antennae and tarsi relatively short. For data on standardized body length, and ratios M 1/P 1, P 1/E 1, and Ant. Art. 3 w/1, see Tables 1 to 4. For data on variation in the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture of elytra with meshes indistinct, markedly transverse. Supraorbital setigerous punctures 2 pairs; labrum with four marginal setae. Pronotum as in Fig. 7A; anterior margin truncate; hind angles acute; base broad, sides rounded, not sinuate. Male front tarsus not expanded, without adhesive vestiture ventrally. Elytra as in Fig. 7A, not vaulted (Fig. 7B); lateral margin sinuate preapically, apical angles rounded, without spines; striae distinctly punctate apically, indistinctly so anteriorly.

Male genitalia with median lobe (Fig. 15A) in lateral aspect with apical portion short and bent ventrally rather markedly, in dorsal aspect slightly sinuate on left side (Fig. 15B). Endophallus with C-sclerite, only.

Geographical affinities. – This species seems to be sympatric with *C. spinicauda.* Specimens of both bear the same information on their respective locality labels (Fig. 23).

Relationships. – This species shares with *C. orizabae* a number of features suggesting at first a close relationship between the two species. Most of these, however, are judged to be symplesiotypic, and thus not indicative of close relationship. For details, see the section on phylogeny, below. Probably *C. lobipennis* is near the ancestor of the subgenus *Cyrtolaus*, as suggested by possession of plesiotypic conditions for development of the elytral plica and male genitalia.

Material examined. – The type specimen, only.

Cyrtolaus (sensu stricto) subiridescens, new species

The slightly iridescent, slightly vaulted elytra, without or with weakly developed apical spines distinguish specimens of this species from other members of subgenus *Cyrtolaus* having uninterrupted elytral epipleura. Males are distinguished by the short narrow apical portion of the median lobe (Fig. 16A, B; cf. Fig. 17A, B and 18A, B).

Description. – Form as in Fig. 8A. Size moderate for genus, antennae and tarsi relatively long. For data on standardized body length, and ratios M 1/P 1, P 1/E 1, and Ant. Art. 3 w/1, see Tables 1 to 4. For data on variation in the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture meshes of elytra, dense, transverse. Surface shining, elytra faintly iridescent. Supraorbital setigerous punctures 2 pairs. Pronotum as in Fig. 8A; anterior margin subtruncate, hind angles rounded, sides elevated posteriorly. Male with adhesive vestiture ventrally on tarsomeres 1 and 2. Elytra as in Fig. 8A, moderately vaulted (Fig. 8B). Humeri not toothed. Margin with slight preapical sinuation. Apex rounded, or with small blunt projection.

Male genitalia with median lobe as in Fig. 16A and B, apical portion abruptly constricted (lateral aspect), short, narrowly rounded (dorsal aspect). Endophallus with apical C-sclerite, spinous sclerites 2 and 3 dorso-basal in position, and spinous sclerite 1 and ventral lobe well-developed (Fig. 16C and D).

Type material. – Holotype male, labelled: Mex. Chiapas 6.6 mi. n. Pueblo Nuevo 5600′, George E. Ball, D.R. Whitehead. Paratypes, 11 males, 14 females, labelled: 1 female (allotype) same as holotype; male, female, Mex. Chiapas, Yerba Buena Hosp., 1.5 mi. n. Pueblo Nuevo 7200′, cloud forest, June 21, 1972, P.A. Meyer, G.E. Ball; male, female, Mex. Chiapas 3.5 mi. n.e. Tenejapa, ca. 30 mi. e.n.e. Tuxtla Gutierrez, 92°22′, 16°50′, under logs, damp shaded ravine, 7000′ XII.30.72, H. Frania; 2 males, 4 females, Mex. Chiapas, w. Tenejapa, ca. 30 mi. e.n.e. Tuxtla Gutierrez, 92°22′, 16°50′, under rotting planks in damp, deep sink, 7000′, XII.27.72, H. Frania; 2 males, Guatemala, Dpto. Huehuetenango, Cuchumatanes Mts., Rte. 9N, 3 mi. e. San Mateo Ixtatan, 2430 m, VIII.9.74, H.F. Frania, D.R. Whitehead, G.E. Ball; male, 4 females, generally as for preceding specimens, but specifically 7.6 mi. w. Santa Eulalia, 2870 m, VIII.10.74; 4 males, 3 females, generally as for preceding specimens, but specifically 4.8 mi. s. San Juan Ixcoy, 2780 m, VIII.11.74.

Disposition of type material. – The holotype and allotype are in the collections of the USNM. The other specimens are in the following institutions: BMNH; CAS; CNC; IPNM; MNHP; and UASM.

Derivation of specific epithet. – From Latin, *sub* (under, less than), and *iridescens* (iridescent), in allusion to the faint iridescent sheen exhibited by the elytra.

Notes on habitat. – Specimens of this species were collected in tropical cloud forest, either on the ground under logs, or under bark of dead hardwood trees, at elevations from 5600 to 9300 feet.

Geographical affinities. – At Yerba Buena, the single specimen of *C. brevispina* was collected at the same time and in the same general area as were specimens of *C. subiridescens.* Thus these two must be regarded as sympatric, at least in this area. They are also parapatric with *C. grumufer,* specimens of which were collected down-slope at 6000 and 5100′, in wet oak-pine-sweet gum forest.

Relationships. – The characteristics of this species suggest that it is the most primitive of those whose members possess an uninterrupted elytral epipleuron. Thus, it stands as the sister species to the stock that gave rise to the more derived species.

Geographical distribution. – The range of this species is the Central Highlands of Chiapas (Fig. 23), and the adjacent Cuchumatanes Mountains of Guatemala.

Material examined. – 26 specimens, all in the type series.

Cyrtolaus (sensu stricto) brevispina, new species

The single known specimen of this species resembles in appearance specimens of *C. furculifer, C. newtoni* and *C. ricardo* (Fig. 11A; cf. Fig. 10A and 12A), but is readily distinguished from these by characteristics given in the key.

Description. – Form as in Fig. 11A. Size larger than average for genus. Antennae and tarsi elongate. For data on standardized body length, and ratios M 1/P 1, P 1/E 1, and Ant. Art. 3 w/1, see Tables 1 to 4. Variation in the relationship between SBL and M 1/P 1 is presented in Fig. 24.

Microsculpture of elytra with meshes isodiametric. Dorsal surface shining. Supraorbital setigerous punctures 1 on left side, 2 on right side. Pronotum as in Fig. 11A, anterior margin very shallowly incised, posterior margin angularly incised, pronouncedly; sides arcuate, explanate and elevated slightly, more so posteriorly than anteriorly; posterior angles about rectangular, not produced, setae distinctly anterad of hind angles. Male with front tarsomeres narrowly expanded, tarsomeres 1 and 2 with adhesive vestiture ventrally. Elytra as in Fig. 11A, not markedly vaulted posteriorly (Fig. 11B); humeri narrowly rounded; lateral margin postero-laterally markedly sinuate, apical angles each with very short spine; striae finely punctate, discal intervals moderately convex. Anal setae 4.

Male genitalia with median lobe as in Fig. 19A and B, apical portion similar to that of *C. ricardo* (cf. Fig. 18A and B); endophallus with well developed C-sclerite and spinous sclerites 1-3; sclerites 2 and 3 basal in origin, of average length.

Type material. – Holotype male, labelled: MEX. Chiapas Yerba Buena Hosp., 1.5 mi. n. Pueblo Nuevo, 7200′, cloud forest, VI.21.72, Ball-Meyer. The specimen is in the USNM collections.

Derivation of specific epithet. – From Latin, *brevis* and *spina* meaning short spine, in allusion to the apical spines of the elytra.

Note on habitat. – This specimen was collected under a log on the ground in a tropical cloud forest.

Geographical affinities. – This species and *C. subiridescens* were collected in the same patch of cloud forest, on the same day and at about the same elevation. Thus the two species appear to be microsympatric.

Relationships. – This is the sister species to the stem group ancestral to *C. newtoni-ricardo-spinicauda-furculifer-grumufer*, as suggested by the plesiotypic form and position of the male genital sclerites.

Geographical distribution. – Known only from the type locality. See Fig. 23.

Cyrtolaus (sensu stricto) newtoni, new species

The single specimen of this species is most like specimens of *C. ricardo* in body form, but the pronotum of the former is proportionately longer and narrower (Table 2, and Fig. 24), and less flattened laterally, and the apical spines of the elytra are short as in *C. brevispina.*

Description. – Size small for subgenus *Cyrtolaus.* For data on standardized body length and ratios M 1/P 1, P 1/E 1 and Ant. Art. 3 w/1, see Tables 1 to 4. For the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture of elytra with meshes isodiametric. Dorsal surface shining. Supraorbital setigerous punctures two pairs. Pronotum as in Fig. 10C, anterior margin very shallowly incised, posterior margin subtruncate, lateral margins slightly elevated, more so posteriorly than anteriorly, posterior lateral angles acute. Elytra in general form as in Fig. 10A, slightly vaulted posteriorly (cf. Fig. 10B); humeri narrowly rounded, lateral margins with slight preapical sinuation, apical angles each with short spine (Fig. 10D). Striae very finely punctate especially anteriorly, discal intervals subcostate toward apex only.

Type material. – Holotype female, labelled: Mexico Oaxaca 22.4 mi. s. Valle Nacional 5600′, 12 Aug. 1973; under bark of thin-barked tree; A. Newton, Collector (MCZ).

Derivation of specific epithet. – This is based on the surname of Dr. A. Newton, a specialist on Middle American staphylinid beetles, to whom we express our appreciation for collecting the only specimen of this species, and making it available to us.

Note on habitat. – This specimen was collected in a narrow steep barranca, on the ground, in a cloud forest.

Geographical affinities. – This species is allopatric to all other species of the genus. Its range is south of the known range of subgenus *Ithytolus*, and north of the known range of all other species of *Cyrtolaus (s. str.).*

Relationships. – This species is regarded as the sister species of the *C. ricardo-spinicauda-furculifer-grumufer* stock.

Geographical distribution. – Known only from the type locality (Fig. 23).

Cyrtolaus (sensu stricto) ricardo, new species

In body form (Fig. 10A) specimens of this species resemble most closely the types of *C. newtoni* and *C. brevispina*, but the pronotum is proportionately shorter and the apical spines of the elytra are much longer.

Description. – Form as in Fig. 10A. Size average for genus. For data on standardized body length, and ratios M 1/P 1, P 1/E 1, and Ant. Art. 3 w/1, see Tables 1 to 4. For variation in the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture of elytra with meshes isodiametric. Dorsal surface shining. Supraorbital setigerous punctures two pairs. Pronotum as in Fig. 10A, anterior margin very shallowly incised, posterior margin subtruncate, lateral margins slightly elevated, more so posteriorly than anteriorly; posterior angles acute, generally as illustrated but less acute in some specimens. Elytra as

in Fig. 10A, slightly vaulted (Fig. 10B); humeri narrow, rounded; lateral margin with slight preapical sinuation, apical angles each with prominent spine; striae finely punctate, discal intervals subcostate toward apex, only.

Male genitalia with median lobe as in Fig. 18A and B, apical portion narrower and shorter than in *C. spinicauda* (Fig. 18B, cf. Fig. 17B). Endophallus with C-sclerite, ventral lobe and spinose sclerites 1-3 well developed, 2 and 3 elongate, strap-like, basal in position. Three males dissected.

Type material. – Holotype male, labelled: MEX. Chiapas Volcan Tacaná, s.e. slope, cloud forest, litter 7800′, VII.22 and VIII.3.72 (G.E. Ball), Paratypes, 14 males, 9 females: 7 males, 7 females (one, allotype) labelled same as holotype; 5 males labelled as holotype, but date July 2-3; male, Tacaná, Sumidero San Antonio, VII.24.72, 9000-10,000′, male, Tacaná, n. Union Juarez VII.28.72, at 7000′; and 2 females, GUATEMALA, Departmento San Marcos, ridge 1.5 km w. El Rincon, 2730-2780 m, XI.8.1974, in log, J.F. Lynch (USNM).

Disposition of type material. – Holotype, allotype and male and female paratype from type locality (USNM); 2 males in each of CAS, CNC and IPNM; 2 males, 1 female in each of BMNH and MCZ: male, female (MNHP); and 2 males, 2 females (UASM). The Guatemala specimens were returned to USNM.

Derivation of specific epithet. – A noun in apposition, based on the given name of a guide and citizen of Union Juarez, Chiapas, Sr. Ricardo Morales, who assisted in finding and collecting specimens of this species.

Notes on habitat. – As indicated by label data, specimens were collected under logs and in leaf litter, on damp ground, in dense wet cloud forest. The beetles were scarce at higher elevations (9000 feet and more) and did not occur in open places or in coniferous forests.

Geographical affinities. – This species and *C. furculifer* Bates are parapatric. Both were collected on Tacaná, but the latter species was found at a much lower elevation.

Relationships. – This species is regarded as the sister species of the *C. spinicauda-furculifer-grumufer* stock, as suggested by common possession of long elytral spines.

Geographical distribution. – This species is known from Volcan Tacaná, Chiapas, on the Mexican-Guatemalan border, and from the adjacent portion of Guatemala (Fig. 23).

Cyrtolaus (sensu stricto) spinicauda Bates, 1882

Cyrtolaus spinicauda Bates, 1882: 100. LECTOTYPE male (here selected), labelled: TYPE, H.T. [circular label, ringed in red]; Purula Guatemala Champion; BCA Col. I. 1. Cyrtolaus spinicauda Bates; Cyrtolaus spinicauda Bates [handwritten]; BMNH; paralectotypes, 2 females, both collected at San Geronimo, Guatemala, one in BMNH, one in MNHP. TYPE LOCALITY: Purula, Guatemala. – Csiki, 1931: 766.

The broadly rounded sides of the pronotum and high-domed elytra with grossly punctate striae distinguish this species from other members of the genus.

Description. – Form as in Fig. 9A. Size average for genus, antennae and tarsi relatively elongate. For data on standardized body length, and ratios M 1/P 1, P 1/E 1 and Ant. Art. 3 w/1, see Tables 1 to 4. For data on variation in the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture of elytra with meshes isodiametric, small, lines coarser than on head, surface shining. Supraorbital setigerous punctures 2 pairs. Pronotum as in Fig. 9A, anterior margin incised, hind angles rounded, sides broadly rounded, posteriorly strikingly broadly explanate. Male with tarsomeres 1 and 2 of anterior tarsus with adhesive vestiture ventrally. Elytra as in Fig. 9A, strongly vaulted (Fig. 9B); humeri rounded; margin with slight preapical sinuation, apical angles each with well developed spine; striae coarsely punctate, intervals crenulate laterally, distinctly carinate.

Male genitalia with median lobe as in Fig. 17A and B. Apical portion moderately elongate, broadly rounded (dorsal aspect), narrowed, sinuate (lateral aspect). Endophallus with C-sclerite and spinose sclerites 1-3 and ventral lobe well developed; sclerites 2 and 3 long, strap-like, attached dorso-basally.

Note on habitat. – The single specimen for which we have ecological data was collected in a cloud forest, under a hardwood log.

Geographical affinities. – The range of this species is at the known southern periphery of *Cyrtolaus*. This species and *C. lobipennis* are at least parapatric and possible sympatric, at San

Geronimo, Guatemala. Although *C. spinicauda* and the related *C. ricardo* are in the same system of highlands, they have not been collected together.

Relationships. – Members of this species share with those of *C. furculifer* and *C. grumufer* prominent pronotal front angles, but are plesiotypic in having two pairs of supraorbital setae and non-tumescent elytral interval 2. Thus, we regard *C. spinicauda* as the sister species of these two species.

Geographical distribution. – This species is known only from the Guatemalan Highlands in Alta Verapaz and Baja Verapaz (Fig. 23).

Material examined. – Total 5 (including 3 types). Locality of type material is indicated in the section on synonymy. The other specimens, a female and a set of elytra were collected in the following locality. GUATEMALA Alta Verapaz 59.5 kil. s. Coban, 4925′, May 31,1973, T.L. and L.V. Erwin (USNM).

Cyrtolaus (sensu stricto) furculifer Bates, 1882

Cyrtolaus furculifer Bates, 1882: 99. LECTOTYPE female (here selected), labelled: Type HT [circular, ringed with red]; Cerro Zunil, 4-5000 ft. Champion; BCA Col. I. 1. Cyrtolaus furculifer Bates; Cyrtolaus furculifer Bates [handwritten] (BMNH). Paralectotypes 2: male, locality same as that of lectotype, (MNHP); female (teneral), locality same as that of lectotype, but labelled 4000 ft (BMNH). TYPE LOCALITY. – Cerro Zunil, Guatemala. – Csiki, 1931: 766.

The head, with a single pair of supraorbital setae, elytra vaulted (Fig. 12B), with intervals 5-7 sub-cordate, and apices of intervals 2 and 3 swollen and elevated are sufficient to distinguish specimens of this species from all other known members of the genus.

Description. – Form as in Fig. 12A. Size large for genus. Antennae and tarsi elongate. For data on standardized body length and ratios M 1/P 1, P 1/E 1 and Ant. Art. 3 w/l, see Tables 1 to 4. For variation in the relationship between SBL and M 1/P 1, see Fig. 24. Microsculpture of elytra with meshes isodiametric. Dorsal surface shining. Supraorbital setae single pair. Pronotum as in Fig. 12A; anterior margin shallowly incised, posterior margin truncate medially, slightly incised laterally; lateral margins broadly rounded, sides explanate, elevated more posteriorly than anteriorly; anterior angles prominent; hind angles acute, small slightly projected. Male with front tarsomeres 1-4 narrowly expanded, tarsomeres 1 and 2 with adhesive vestiture ventrally. Elytra as in Fig. 12A, vaulted posteriorly, as in Fig. 12B; striae moderately coarse otherwise as described above.

Male genitalia with median lobe as in Fig. 21A and B, apical portion short, tapered, apex narrowly rounded (dorsal aspect, Fig. 21B), sinuate (lateral aspect 21A). Endophallus (Fig. 21C) with C-sclerite lightly sclerotized, ventral lobe small, spinose sclerite 1 well developed, spinose sclerites 2 and 3 broad, basal in position.

Note on habitat. – The specimens from Chiapas were collected on the slopes of a deep canyon, on the ground, under logs, in a coffee plantation. The vegetation was probably originally tropical montane forest.

Geographical affinities. – This species and *C. ricardo* are parapatric on Volcan Tacaná, with the latter species occurring at a higher elevation. Elsewhere, *C. furculifer* is the only species of the genus known from Cerro Zunil, Guatemala.

Relationships. – This species is regarded as the sister species of *C. grumufer* new species, based on general structural similarity and the synapotypic features of a reduced number of supraorbital setigerous punctures, costate lateral elytral intervals and tumescent apical portion of interval 3.

Geographical distribution. – This species is known from southeastern Chiapas and southwestern Guatemala (Fig. 23).

Material examined. – Six specimens (including type material), male and 5 females. In addition to the type locality, specimens are known from: MEX, Chiapas, Union Juarez, Barranca Providencia, on Volcan Tacaná, about 5000′, July 30, 1972, G.E. Ball (UASM); and Chiapas, Finca La Isle (F. Psota Coll, FMNH).

Cyrtolaus (sensu stricto) grumufer, new species

A combination of large size (13.0 mm or more in standardized body length), single pair of supraorbital setigerous punctures, subcostate elytral intervals 5-7 and tumescent apical portion of interval 2 distinguish members of this species from all others except *C. furculifer.* Members of the last-named species have both elytral intervals 2 and 3 elevated near apex.

Description. – Form as in Fig. 13A. Size large. For data on standardized body length and ratios M 1/P 1, P 1/E 1 and Ant. Art. 3 w/l, see Tables 1 to 4. For data on variation in the relationship between SBL and M 1/P 1, see Fig. 24.

Microsculpture of pronotum with meshes very dense, more so than in any other species of the genus; of elytra, meshes isodiametric, small, lines fine. Dorsal surface generally shining, pronotum pronouncedly sericeous. Single pair of supraorbital setigerous punctures. Pronotum as in Fig. 13A, anterior margin excised, posterior margin trisinuate; lateral margins rounded, sides elevated and flared posteriorly, anterior angles prominent. Male with front tarsomeres narrowly expanded, tarsomeres 1-2 with adhesive vestiture ventrally. Elytra as in Fig. 13A, vaulted in lateral aspect (Fig. 13B). Humeri narrowed, angulate, lateral margin slightly sinuate preapically; striae moderately coarsely punctate, intervals convex, 5-7 subcostate; interval 2 tumescent preapically.

Male genitalia with median lobe as in Fig. 20A and B, apical portion long, broad, broadly subtruncate (dorsal aspect Fig. 20B), sinuate (lateral aspect, Fig. 20A). Endophallus with C-sclerite lightly sclerotized, ventral lobe and spinose sclerite 1 absent, spinose sclerites 2 and 3 medio-lateral in position (Fig. 20C).

Type material. – Holotype male, labelled: MEX. Chiapas Yerba Buena Hosp., 1.5 m. n. Pueblo Nuevo, 5100-6000′, June 21-22, 1972, P.A. Meyer, G.E. Ball, collectors. Paratypes 5, 2 males and 2 females (1 allotype), labelled as holotype; 1 male from same locality but labelled specifically 5100′, and VI.22.72.

Disposition of type material. – The holotype and allotype are in the collections of the USNM. A male and female paratype are in UASM, and a male paratype is in each of BMNH and MNHP.

Derivation of specific epithet. – Latin, *grumus* (mound), and *-fer* (suffix meaning bear), in allusion to the swollen apical portion of elytral interval 2.

Note on habitat. – The type series was collected in wet pine-oak-sweet gum forest, on the property of the Yerba Buena Mission, on a west facing slope. Most of the specimens were collected at the lower elevation (5100′), at the bottom of a ravine just below the mission buildings. There was an abundance of cover on the ground, and the beetles were under the bark of pine logs or on the ground, under large, partly buried logs.

Geographical affinities. – This species, *C. subiridescens* and *C. brevispina* occur in the same general area, but the latter 2 species were collected at higher elevation and in cloud forest. Thus, *C. grumufer* is parapatric with these species. It is allopatric with its close relative, *C. furculifer.*

Relationships. – Structurally, this is the most highly evolved species of the genus. It is regarded as the sister species of *C. furculifer.*

Material examined. – Type material, only.

EVOLUTIONARY CONSIDERATIONS

Morphological Evidence

Proportions. – Examination of body form suggested that larger specimens had proportionately longer pronota. To test this, a ratio was calculated using values for mandible length divided by pronotal length. Values for the ratio would be relatively lower for specimens with longer pronota. These values were plotted against SBL, and the results are presented in Figure 24.

This figure illustrates three points: first, for the subgenus *Cyrtolaus*, there is a negative relationship between values for the ratio and those for the measurement, indicating that larger specimens have proportionately larger pronota. Second, two groups are evident: *C. orizabae* (subgenus *Ithytolus*), and subgenus *Cyrtolaus*. Specimens of *C. orizabae*, although relatively small, have proportionately longer pronota. Third, in the subgenus *Cyrtolaus*, the more apotypic species are the ones with the proportionately longer pronota (*C. furculifer* and *C. grumufer*; see Fig. 24 and 25). (The single specimen of *Cyrtolaus newtoni* occupies an exceptional and thus

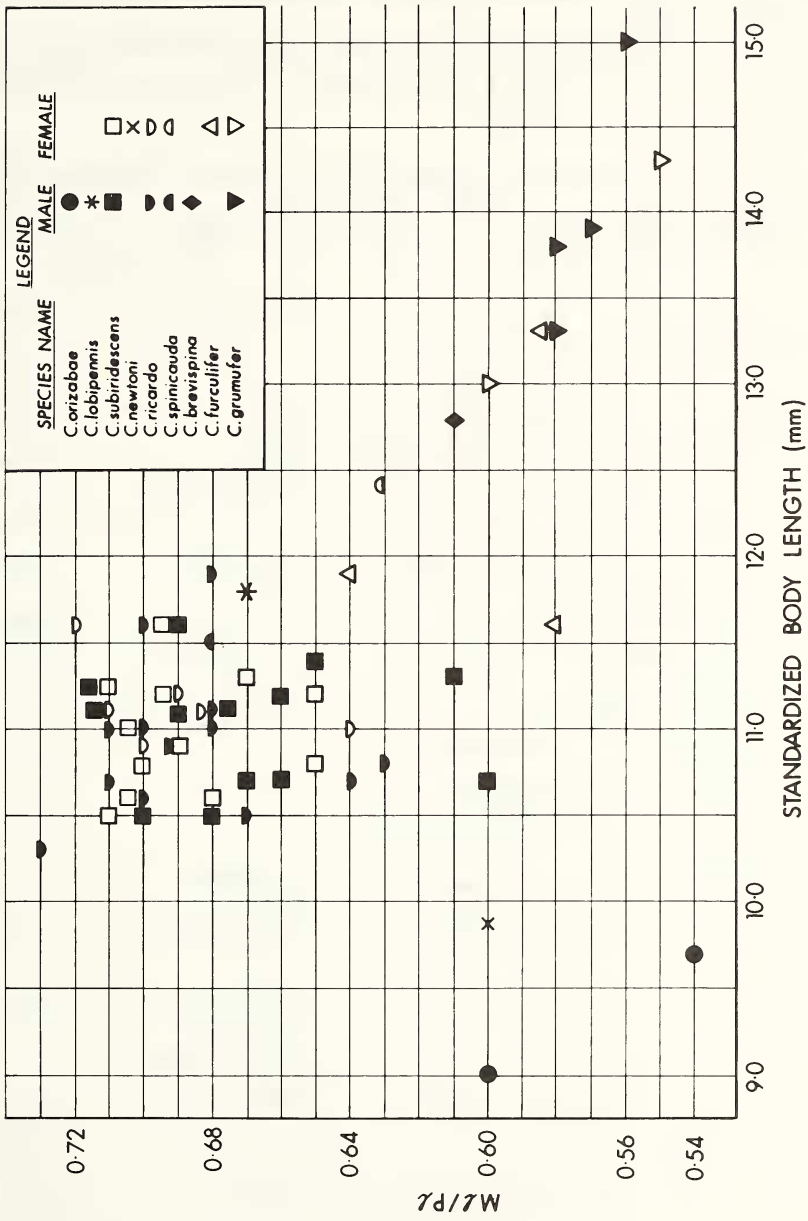


Fig. 24. Graph illustrating the relationship between values for standardized body length and the ratio M 1/P 1 for the species of *Cyrtolaus* Bates.

equivocal, position. It may represent a third slope, intermediate between that for *Ithytolus* and that for the other members of subgenus *Cyrtolaus*, or it may be on the periphery of one or the other of these two slopes. Data for additional specimens will provide the answer.)

These affinities are interpreted in phylogenetic terms as follows. Within the genus, selection has acted to produce an increase in overall size, and a disproportionate increase in length of pronotum. The second trend has generally paralleled size increase in *Cyrtolaus (sensu stricto)* though *C. newtoni* may be an exception, but in *Ithytolus* the second trend seems to have been independent of the first.

Study of the functional significance of a proportionately larger pronotum may contribute to understanding some of the selective forces that have led to the structural divergence represented among the extant species of *Cyrtolaus*.

Table 5. Phylogenetic Classification of Character States of Selected Characteristics of *Cyrtolaus* Bates.

No.[1]	Characteristic	Character State	
		Plesiotypic	Apotypic
1	Labrum, No. setae	6	4
2	Antennae (& tarsi)	short	elongate
3	Supraorbital setae	2 pairs	1 pair
4	Pronotum: anterior bead	present	absent
5	Pronotum: posterior setae, position	near hind angles	remote from hind angles
6	Pronotum: front angles	not strongly produced	strongly produced
7	Front tarsi, male	adhesive vestiture on articles 1-2	without adhesive vestiture
8	Elytra	not fused	fused
9	Elytral plica	epipleuron crossed	epipleuron not crossed
10	Elytra: strial punctation	moderate	impunctate finely punctate 10′ grossly punctate 10″
11	Elytron: apex	rounded, or angulate	spine short spine long 11′
12	Elytron: interval 2, apically	not tumescent	tumescent
13	Elytron: microsculpture	isodiametric	transverse
14	Anal setae	male, 1 pair female, 2 pairs	multiple
15	Male genitalia: endophallus sclerites 2 & 3	absent	basal, short basal, long 15′ lateral medial 15″
16	Male genitalia: endophallus sclerite 1	absent	present absent 16′

1. Code number, as used in Figure 25.

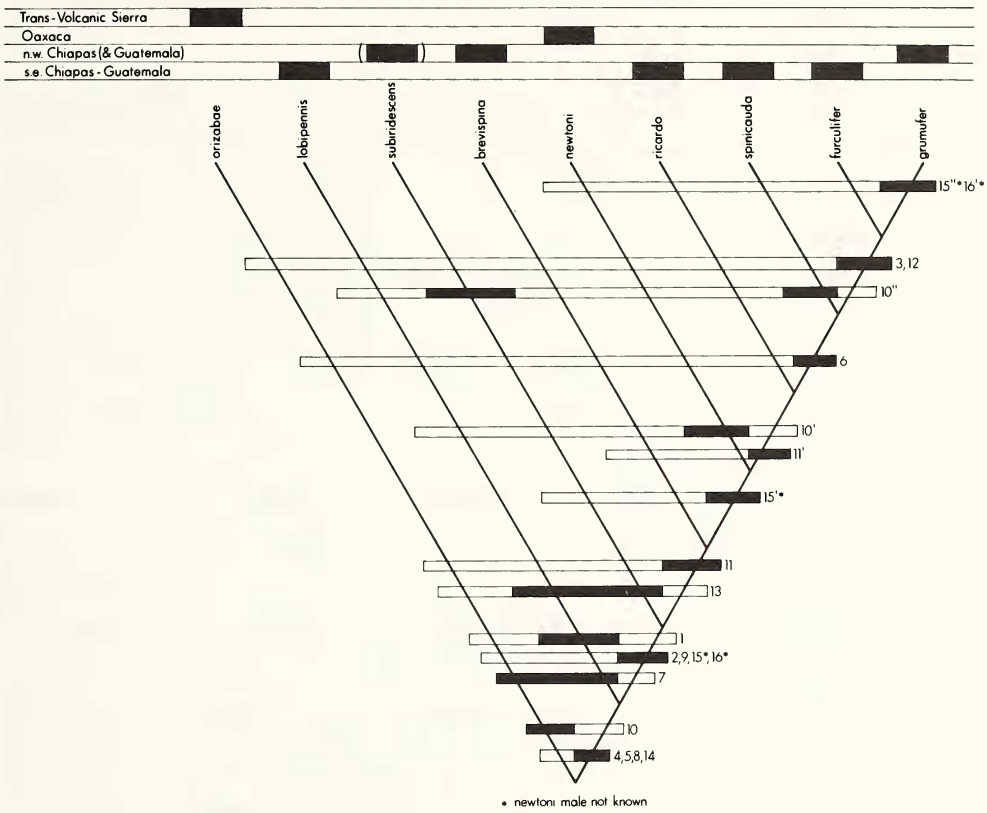


Fig. 25. Phylogenetic diagram and generalized distribution for the species of *Cyrtolaus* Bates.

Phylogeny of Cyrtolaus. – The most parsimonious phylogeny that we can reconstruct for *Cyrtolaus* is outlined in Fig. 25. In this standard phylogenetic tree, the vertical axis represents time and the horizontal axis represents divergence, but neither the angles nor the precise positions of the branches are intended to represent amount of divergence in time or structure. This diagram and the system of notation in Table 5 and the following discussion, are modified from those of Ball and Erwin (1969) and Ball and Nègre (1972) to simplify representation of those apotypic conditions thought to have arisen more than once. Designations of characters as two-state or multi-state, and inferences concerning plesiotypy and apotypy, are as discussed by Ball and Nègre (1972). The only complex or multi-state characters are in punctation of elytral striae, in form of elytral apex, and in armature of the male endophallus. In the diagram, each horizontal bar represents a character, and shaded portions represent the apotypic character state; incomplete bars represent segments of morphoclines. Numeral designation and phylogenetic classification of characters and character states are presented in Table 5. Evolution of multi-state characters is discussed, below.

Punctation of the elytra is probably a combination of 2-state characters rather than a morphocline, but if it were treated as a single multi-state character the impunctate condition would be considered plesiotypic and the reconstructed phylogeny would not be altered.

As interpreted here, the character states of the male endophallus (15,16) represent a single, complex morphocline sequence: sclerites 2 and 3 are primitively absent. and develop successively as short and baso-lateral through long and baso-lateral to short and medio-lateral; sclerite 1 is primitively absent and after developing in an early stock is secondarily lost.

In our reconstruction of *Cyrtolaus* phylogeny, 14 apotypic conditions arose just once and three others arose twice. We suspect that our reconstruction is, if not wholly accurate, at least not radically wrong. It is in agreement with distributional data, and, further, two of the three apotypic conditions proposed to have arisen twice are thought to have done so in consecutive branches. This reconstruction was tested by simplified numerical methods (Willis, 1971), as were similar reconstructions based on variant assumptions about the structure of the male genitalia of *C. newtoni*; this reconstruction is the most parsimonious of those tested, but even if our assumptions prove incorrect only the middle section of the reconstruction need be altered. Another reconstruction was based on the assumption that *C. brevispina* normally has one rather than two pairs of supraorbital setae (the only known specimen has 1.5 pairs!), but failed when tested for parsimony.

Bates (1884) placed *C. lobipennis* with *C. orizabae (=anomalus)* in *Ithytolus*, leaving only the species without crossed elytral epipleura in *Cyrtolaus*. We accept *Ithytolus* as a subgenus of *Cyrtolaus*, but for morphological and geographic reasons place *C. lobipennis* in *Cyrtolaus s. str.* The fused elytra of all species of *Cyrtolaus s. str.* imply not only antiquity but greatly reduced vagility, so that placement of *lobipennis* in *Cyrtolaus s. str.* reflects a reasonable and probably natural vicariance between *Ithytolus* and *Cyrtolaus.* If *Ithytolus* and *Cyrtolaus* of Bates were treated as sister groups (that is, if *lobipennis* is kept in *Ithytolus*), convergence in character 7 would be eliminated but new convergences would arise in characters 4, 5, 8, and 14. Convergence in character 7 is not as remarkable as it might appear, because even in species with distinct specialized adhesive vestiture on the ventral surfaces of the basal articles of the male front tarsus this vestiture is not as strongly developed as in most other Pterostichini.

Convergence in character 13—transverse elytral microsculpture—is not remarkable among the Pterostichini; but if *C. lobipennis* and *C. subiridescens* were regarded as sister species to eliminate that convergence, additional convergences would result in characters 2, 9, and 15.

Two species (*C. subiridescens* and *C. spinicauda*) have grossly punctate elytral striae. This character, however, is varied within the genus and probably has little significance: though gross punctation is not a common feature in Pterostichi, variation in strial punctation is common. Treatment of *C. subiridescens* and *C. spinicauda* as sister species requires additional convergences in characters 11 and 15.

Zoogeography

The sparse locality data impose severe limitations on an attempt to identify distribution patterns and to interpret them in an historical context. Nonetheless, the outline of a pattern seems evident, and it seems important to draw this to the attention of the reader. So, we present a bare skeleton of evolutionary history of *Cyrtolaus*. This is best appreciated in terms of general principles of evolution of mountain faunas (Darlington, 1971), and against a background of geological and biotic history of Middle America (see, for example, Duellman, 1970; Whitehead, 1972; Goulet, 1974; Halffter, 1974; and Ball, 1975).

The distribution pattern. – The locality records for a species are taken as evidence of the occurrence of that species not only at the places in question but also in suitable habitats throughout the mountain system of which the particular localities are a part. This is indicated in Fig. 25, where we classify the ranges of species as "Transverse-Volcanic Sierra; Oaxaca; northwestern Chiapas; and southeastern Chiapas-Guatemala". The species of *Cyrtolaus* are confined to an area including southern Mexico and western Guatemala (Fig. 22). This is essentially "nuclear Central America" (Duellman, 1970). Because members of this genus are mainly inhabitants of cloud forests mostly on the seaward slopes of mountains, it seems likely that conditions in the lowlands, on the lower slopes of mountains, and on the more exposed higher, drier or inland slopes, are inimical to the beetles. The lowland areas presently seem to be barriers to dispersal enhanced in effectiveness by the inability of the beetles to fly. Thus, one might expect each of a series of proximate mountain systems to have a more or less distinctive *Cyrtolaus* fauna. This expectation is realized. In the mountains south of the Isthmus of Tehuantepec, seven species occur; north of the Isthmus, one species is known from the highlands of Oaxaca; and still farther north, on the Caribbean slopes of the Trans-Volcanic Sierra is yet another species. No single species is common to any two of these areas. Further, within the Chiapan-Guatemalan mountain systems (Fig. 23), allopatry is the rule, although there is one confirmed instance of sympatry (*C. subiridescens* and *C. brevispina* at Yerba Buena), a possible second instance (*C. lobipennis* and *C. spinicauda* at San Geronimo), and two instances of parapatry (*C. subiridescens-brevispina* at higher elevation, *C. grumufer* in the same area at lower elevation; and on Tacaná, *C. furculifer* at lower elevation, and *C. ricardo* at higher elevations). Additional collecting is certain to alter this pattern, but probably not to completely falsify it.

Historical aspects. – Although *Cyrtolaus* is probably an old group, as suggested by no evident extant sister group, and by its many apotypic features, including confinement to mountain forests, flightlessness and associated loss of wings, reduction of the metathorax, and fusion of the elytra - nevertheless the extant species may not be that old because they seem, on the whole, to be closely related and to exhibit a fairly orderly distribution pattern (closest relatives allopatric; range overlap generally limited). Possibly, evolution of the extant fauna has taken place during the later Tertiary and Quaternary.

Because we cannot identify the sister group of *Cyrtolaus*, we cannot specify from which direction (north or south) the ancestral stock of this genus reached nuclear Middle America. Probably this stock was adapted to life in the tropical lowlands, evolved upland forms, eventually became extinct in the former areas, and its upland stocks became adapted to life in cloud forests. We suggest that by Miocene time, there were two flightless mountain-adapted stocks of *Cyrtolaus*, one on each side of what might have been an imposing barrier: the Isthmus of Tehuantepec. The northern group retained most of the plesiotypic features, and gave rise to the subgenus *Ithytolus*, known from a single extant species, *C. orizabae.* The southern group underwent more differentiation, to become the ancestor of subgenus *Cyrtolaus.* If our phylogeny is correct, the geographical correlates (Fig. 25) suggest this sequence of events: division of the ancestral stock (designated as Ancestor A) into a lineage east of the Rio Chixoy which gave rise to *C. lobipennis,*

and one to the west (Ancestor B). The Ancestor B lineage split into two groups, one in the central highlands of Chiapas, and the Cuchumatanes Mountains, which gave rise to *C. subiridescens*, and a more southern one (Ancestor C), which eventually became widespread. Ancestor C then split into two stocks: one in the southeast (Ancestor D, Sierra Madre de Chiapas and associated mountains in Guatemala) and one to the northwest, which gave rise to *C. brevispina.* The Ancestor D lineage succeeded in crossing the Isthmus of Tehuantepec, possibly during the early Pleistocene, when conditions may have been suitable to the normally upland forests in the lower hills of the Isthmus (see Duellman, 1970), became isolated there, and gave rise to *C. newtoni;* meanwhile the Sierra Madrean stock in Chiapas and Guatemala gave rise to Ancestor E. Ancestor E then dispersed, with *C. ricardo* becoming differentiated in the southeast and Ancestor F arising in the northwestern mountains. Ancestor F then dispersed and differentiated, to produce *C. spinicauda* to the east of the Rio Chixoy drainage and Ancestor G in the northwestern mountains. The latter re-dispersed, its descendant stocks becoming isolated to produce *C. furculifer* in the southern mountains and *C. grumufer* in the Chiapan highlands.

Coincidentally with this system of dispersals and re-dispersals, isolation and differentiation, the putative earlier inhabitants of each mountain system moved upward as later invaders became established.

Overall, the system proposed is complex, but no more so than those proposed for various groups of vertebrates inhabiting Middle America (see, for example, Hershkovitz, 1967, for an account of rodent dispersal, and Duellman, 1970, for an account of hylid frogs). Especially important to the development of the pattern have been movements between the major east-west mountain systems, followed by isolation and differentiation. This is our hypothesis. It can be tested both by analogy with the explanations provided for other groups of organisms, and by information obtained from additional field work. We hope that others will be inspired to pursue the lines suggested by this initial essay, and we await the results with interest.

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In the Department of Entomology, University of Alberta, John S. Scott prepared the plates, and drafted the maps and Figures 24 and 25. Preliminary drafts of the manuscript were typed by Susan Hamilton and Twyla Gibson.

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